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CHROMOSOMAL FISSIONS AND PHYLOGENETIC HYPOTHESES: CYTOGENETIC AND ALLOZYMIC VARIATION AMONG SPECIES OF MERIONES (RODENTIA: GERBILLIDAE)

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Phylogenetic hypotheses based on morphological data for many groups of higher vertebrates have been re-examined using data derived from G-banded chromosomes. Studies of G-banded chromosomes are important because G-bands reflect genetic homology and because such data can be useful in understanding relationships among taxa as well as rates of chromosomal evolution (Baker *et al.*, 1987). The use of independent data sets generally is beneficial for several reasons. First, an inherent lack of resolution from one data set at some level of the phylogeny can be offset by using another data set that provides resolution at that level (Arnold *et al.*, 1982). Second, independent data allow for choices between equally or almost equally parsimonious explanations of a data set. Third, using independent data sets can resolve character conflicts by identifying character states that need to be reexamined. However, an independent data set can produce a phylogenetic hypothesis that is quite different from that being tested and thus additional data and re-analysis of available data may be required.

Relationships within the genus *Meriones* have been controversial. Morphological criteria based on such characters as size and shape of the bullae (Chaworth-Musters and Ellerman, 1947; Ellerman, 1941; Pavlinov, 1982) have been questioned as potentially convergent characters by authors who examined nondifferentially stained chromosomes (Nadler and Lay, 1968; Wahrman *et al.*, 1988). Benazzou *et al.* (1982*a*, 1982*b*, 1984) presented data for R-banded chromosomes of six species of *Meriones* and produced trees of relationships of these and other genera of gerbils based on the assumption that "common equals primitive." Benazzou *et al.* (1982*b*) stated that either *M. tristrami* possesses an ancestral karyotype of high diploid number and those of other species of *Meriones* were derived by fusions or, alternatively, that species with high diploid numbers of chromosomes arose from ancestors having low diploid numbers by chromosomal fissions. However, the outgroup method in chromosomal analyses is preferred over "commonality" on both empirical and philosophical grounds and the two methods can yield different phylogenies (Qumsiyeh and Baker, 1988). Qumsiyeh *et al.* (1988) presented G-band data for two species of *Meriones* (*shawi* and *unguiculatus*, both with 2n = 44), *Psammomys obesus* (2n = 48), *Sekeetamys calurus* (2n = 38), and *Desmodillus auricularis* (2n = 52). In that study, the outgroup method was used to analyze chromosomal data and to compare the resulting phylogeny to an electrophoretic data set from the same specimens to arrive at conclusions regarding the rates of protein and chromosomal evolution in these taxa. I herein address data on G-band and allozymic variation of *Meriones crassus* (2n = 60) and *M. tristrami* (2n = 72) and re-evaluate all previously published data on this group in light of the new information.

MATERIALS AND METHODS

Chromosomal Analyses

G-banding on two species of *Meriones* (*M. tristrami* and *M. crassus*) was performed by the method of Lee and Elder (1980) as modified by Baker and Qumsiyeh (1988). Specimens examined for these two species of *Meriones* are as follows (all voucher material deposited at Texas Tech University). *Meriones tristrami*: Jordan, Amman Gov., Al Muwaqqar, 22 km. E Amman (1 ♂, 1 ♀); Al Ghor, Ghor nimrin, near King Hussein Bridge (2 ♂♂); Northern Gov., 10 km. E Irbid (3 ♂♂, 5 ♀♀). *Meriones crassus*: Jordan, Amman Gov., Al Azraq, 5 km. W Azraq (1 ♂); Egypt, Sinai Gov., El Tor (1 ♂, 1 ♀ born in captivity).

Identification of G-band sequences from gerbils was facilitated by using a standard numbering system developed for gerbil chromosomal arms or linkage groups (Qumsiyeh, 1986). Side-by-side comparisons of all chrosmosomes and chromosomal arms were performed first between metaphases of the same individual, then between those of individuals of the same species, and finally between those of different species and genera. The original karyotypes from several individuals of taxa previously examined (Qumsiyeh and Chesser, 1988) were re-analyzed in light of data presented here on *Meriones crassus* and *M. tristrami.* Additionally, the availability of the G-banded chromosmes of *Meriones tristrami* allowed comparison of numbering systems and identifying homologies to the R-band data of species studied by Benazzou *et al.* (1982*a*, 1982*b*, 1984), because these latter studies used the R-band karyotype of *M. tristrami* for a standard numbering system. Thus, postulated chromosomal rearrangements can be re-evaluated and data added for two species of *Meriones* (*libycus* and *persicus*) by using R-band homologies. Based on comparisons of karyotypes and banding patterns, only a few discrepancies were found in identifying chromosomal rearrangements between my studies and those of Benazzou *et al.* (1982*a*, 1982*b*, 1984). These are further discussed in the results section.

Abbreviations used in figures are as follows: DAU, *Desmodillus auricularis*; MCR, *Meriones crassus*; MLI, *M. libycus*; *MPE, M. persicus*; MSH, *M. shawi*; MTR, *M. tristrami*; MUN, *M. unguiculatus*; POB, *Psammomys obesus*; SCA, *Sekeetamys calurus*; FU, centric fusion; FI, centric fission; EU + , euchromatic addition; PAI, paracentric inversion; PEI, pericentric inversion; d, distal; p, proximal. These abbreviations are used in conjunction with chromosome numbers referring to the proposed homology and standard numbering system for gerbil G-band chromosomal segments (Qumsiyeh, 1986).

Electrophoretic Analyses

Thirty-two presumed loci were assayed by starch gel electrophoresis for the same taxa and individuals used in the chromosomal analysis. Electrophoretic loci examined, abbreviations for loci, techniques, and analyses were as described by Qumsiyeh and Chesser (1988). However, a uniform nomenclature that would change names used for some enzymes has been recommended by the International Union of Biochemistry (1984) as follows: aconitase hydratase (for aconitase), dihydrolipoamide dehydrogenase (diaphorase), fumarate hydratase (fumarase), and aspartate aminotransferase (glutamine oxaloacetate transaminase). Allele frequency data were used to calculate genetic similarities and distances (Rogers, 1972). Matrices of distance values were used to construct trees by the Fitch and Margoliash (1967) algorithm. Cladistic analyses were performed by coding allelic variants as character states and the analyses were performed using a Wagner algorithm (Farris, 1970, 1978), and then subjected to multiple branch swappings using the computer program MacClade (Wayne Maddison and David Maddison). Character state changes were coded as unordered (that is, a change from any state to any other state was

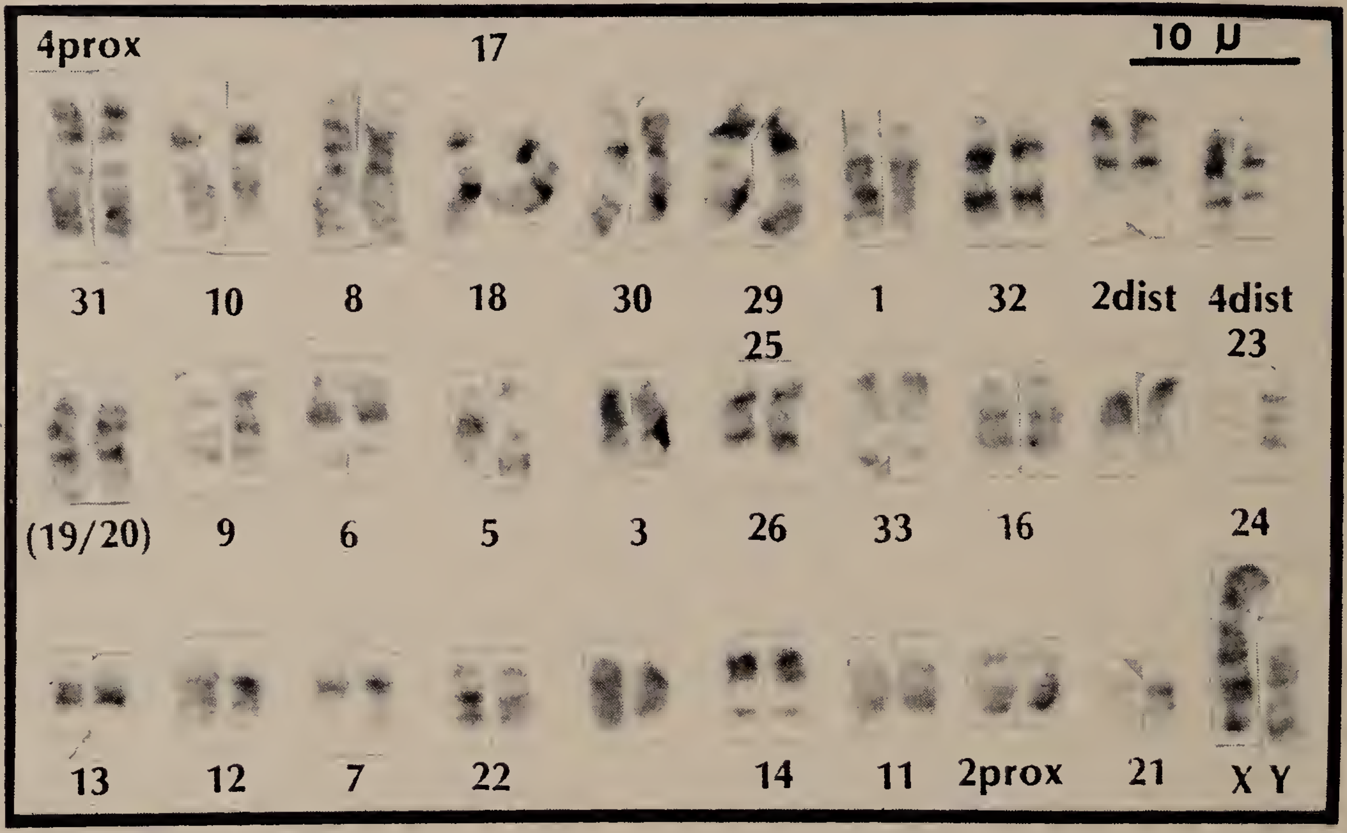

FIG. 1.—G-banded karyotype of a male *Meriones crassus*. Chromosome numbers in this and other figures and tables refer to standard gerbil linkage groups (Qumsiyeh, 1986; Qumsiyeh and Chesser, 1988).

allowed and counted as one step) because there are no *a priori* reasons to polarize transformation series for electrophoretic data.

RESULTS

Chromosomal Analyses

The karyotypes of *Meriones tristrami* (2n = 72, FN = 76-80) and *M. crassus* (2n = 60, FN = 72) show extensive homology to each other and most chromosomes can be assigned numbers referring to their homology with those of other gerbils (Qumsiyeh, 1986; Figs. 1- 2). The G-band data from these two species then were compared to G-band data for *Meriones unguiculatus, M. shawi* (Jordan), *Psammomys obesus, Sekeetamys calurus*, and *Desmodillus auricularis* (Qumsiyeh and Chesser, 1988), and with published R-band data for *Meriones crassus, M. tristrami, M. shawi* (Morocco), *M. unguiculatus, M. libycus, M. persicus*, and *Psammomys obesus* (Benazzou *et al.*, 1982*a*, 1982*b*, 1984). Results of these studies indicated that, with few exceptions, there is extensive agreement between investigations using G-bands and those using R-bands in identification of chromosomes and rearrangements (Table 1). Using the standard gerbil arm numbering system (Qumsiyeh, 1986), these exceptions are as follows. First, fusion ?/31 in *Psammomys obesus* (Qumsiyeh and Chesser, 1988) is identified as 1/31 based on correspondence with the data of Benazzou *et al.* (1982*a*, 1984). Second, chromosomes 21/22, 23/24, and 30 are difficult to identify in

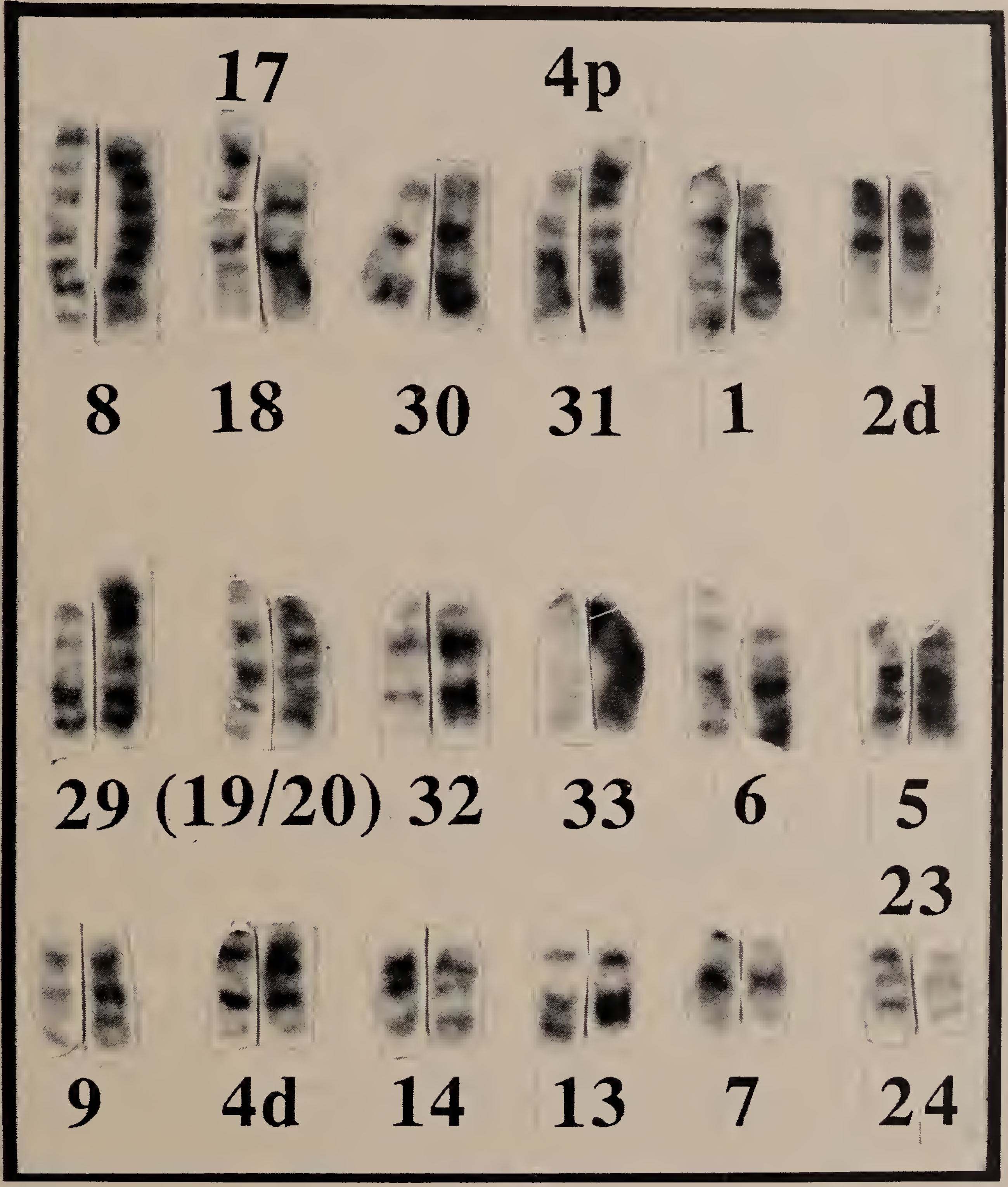

FIG. 2.—Selected chromosomal G-band comparisons between *M. tristrami* (left chromosome of each pair) and *M. crassus*.

R-banding and were either unassigned or misidentified in some taxa reported by Benazzou *et al.* (1982 *a*, 1982*b*).

However, discrepancies between the G-band data for *M. shawi* from Jordan and the R-band data for *M. shawi* from Morocco (Benazzou *et al.*, 1982*b*) clearly were not technical, but rather are due to unique rearrangement differences between the two samples. Unlike the Jordanian *M. shawi* (shown in Table 1), the Moroccan specimen differs by the presence of fused chromosomal arms 1/2d and 5/33 and the absence of fusion 9/31. Because I do not have access to the voucher specimen from Morocco, it is difficult to determine if these karyotypic differences are due to intraspecific variation or if the Moroccan specimen belongs to another species. My results (Table 1) show three

TABLE 1.—*Chromosomal characteristics for six species of* Meriones. *All numbers refer to proposed homology based on standard numbering system for linkage groups in Gerbillidae proposed earlier (Qumsiyeh, 1986) except column listing the corresponding standard numbers of Benazzou* et al. *(1982* a, *1982* b, *1984). Two numbers separated by a comma indicate separate linkage groups; the same separated by a slash indicate the two are fused. The data for* M. shawi *is for Jordanian specimens (Qumsiyeh and* Chesser, 1988) and not for *the Moroccan specimen (Benazzou* et al., *1982* b*).*

		Taxa and chromosomal character states					
Linkage group	Benazzou number	*crassus*	*tristrami*	*unguiculatus*	*shawi*	*libycus*	*persicus*
1	8	1	1	1/(19/20)	1	1	1/2d
2p	29	2p	2p	2p	2p	2p	2p
2d	9	2d	2d	32/2d	2d	2d	1/2d
3/4p	13/25	3,4p/31	3,4p	3/4p	3/4p	3/4p	3/4p
4d	19	4d	4d	4d/11	4d/11	4d/11	4d/11
5	11	5	5	5	5	5/33	5/33
6	12	6	6	6/8	6/(19/20)	6/(19/20)	6/(19/20)
7	20	7	7	7/12	7/12	7/12	7/12
8	5	8	8	6/8	32/8	32/8	32/8
9	1	9	9	9/(27/28)	(9)/31	9/31	9
10	24	EU + 10	10	10	10	10	16/10
11	26	11	11	4d/11	4d/11	4d/11	4d/11
12	14	12	12	7/12	7/12	7/12	7/12
13/14	21/18	13,14	13,14	13/14	13/14	13/14	13/14
15/16	28/16	15,16	15,16	15,16	15,16	15,16	15,16/10
17/18	27/23	17/18	17,18	17/18	17/18	17/18	17/18
19/20	10	(19/20)	(19/20)	1/(19/20)	6/(19/20)	6/(19/20)	6/(19/20)
21/22	3 or 4	21,22	21,22	21/22	21/22	21,22	21,22
23/24	35/31	23/24	23/24	23/24	23/24	23/24	23/24
29	17 + 33	(29)	Fi(29)	(29)	(29)	(29)	(29)
30	30	(30)	(30)	(30)	(30)	(30)	(30)
31	6	4p/31	31	31	(9)/31	9/31	31
32	7	32	32	32/2d	32/8	32/8	32/8
33	22?	33	33	?/33	33	5/33	5/33

autosomal differences between *M. shawi* and *M. libycus* and confirm the earlier data based on hybridization and nondifferentially stained chromosomes (Lay and Nadler, 1969). Similarly, my data for *M. unguiculatus* identify an acrocentric chromosome 5, and that of Benazzou *et al.* (1984) shows a fusion 5/33. Although Qumsiyeh *et al.* (1988) did not identify the small arm fused to 33, it clearly was not 5.

The available chromosomal data for *Meriones* (Table 1) were analyzed in conjunction with data for *Desmodillus auricularis*, *Sekeetamys calurus*,

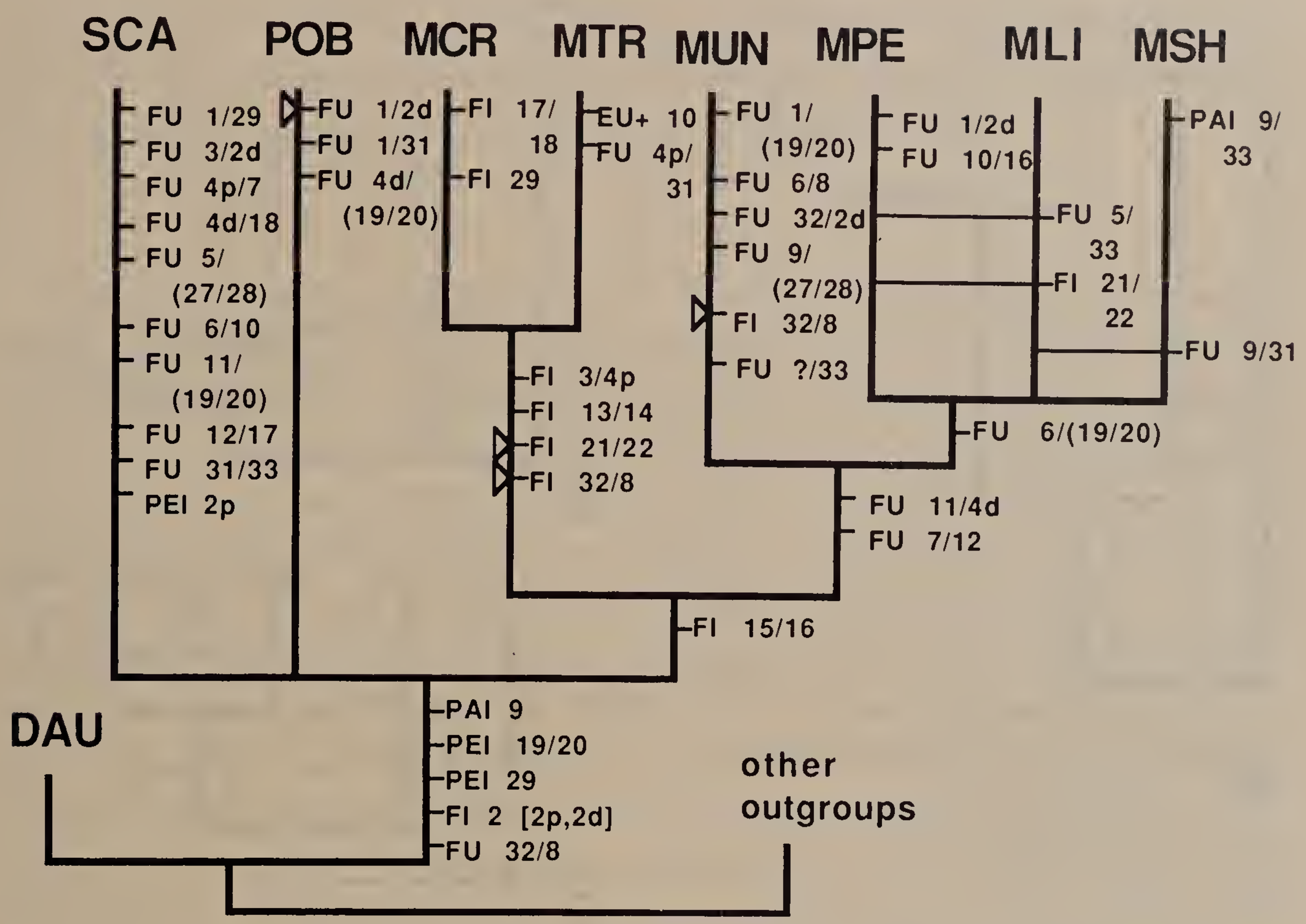

FIG. 3.—A phylogeny for *Meriones, Sekeetamys calurus, Psammomys obesus*, and *Desmodillus auricularis* based on chromosomal data from Table 1 for *Meriones* and from Qumsiyeh and Chesser (1988) for other genera. Triangles (arrow heads) indicate homoplasies (reversals and convergences). Resolving the trichotomy shown would add additional homoplasies.

Psammomys obesus, and outgroup sigmodontines (Qumsiyeh and Chesser, 1988). Figure 3 shows a resulting tree based on minimizing the number of chromosomal fusions and inversions. In this parsimony analysis, I assumed that the probability of independent fusions to yield the same biarmed condition (convergence in centric fusions) is much lower that the probability of fissions. This is because it is highly unlikely that two identical centric fusions became fixed in two independent lineages.

Electrophoretic Analyses

Of the 32 loci examined, only three (EST, GOT-1, and ICD-1) showed fixed differences among the four species of *Meriones*, whereas 20 were monomorphic for these species (Appendix). EST(100) allele is shared between *M. unguiculatus* and *Psammomys obesus*. The two other unique alleles, GOT-1(105) and ICD-1(80), occur in the two taxa for which I had small sample sizes (*M. unguiculatus* and *M. crassus*, respectively). Comparison of intrageneric (in *Meriones*) genetic distances with those among genera of gerbils suggests a close relationships within *Meriones*. For all these analyses, the data shown in the Appendix were analyzed in combination with the available data for

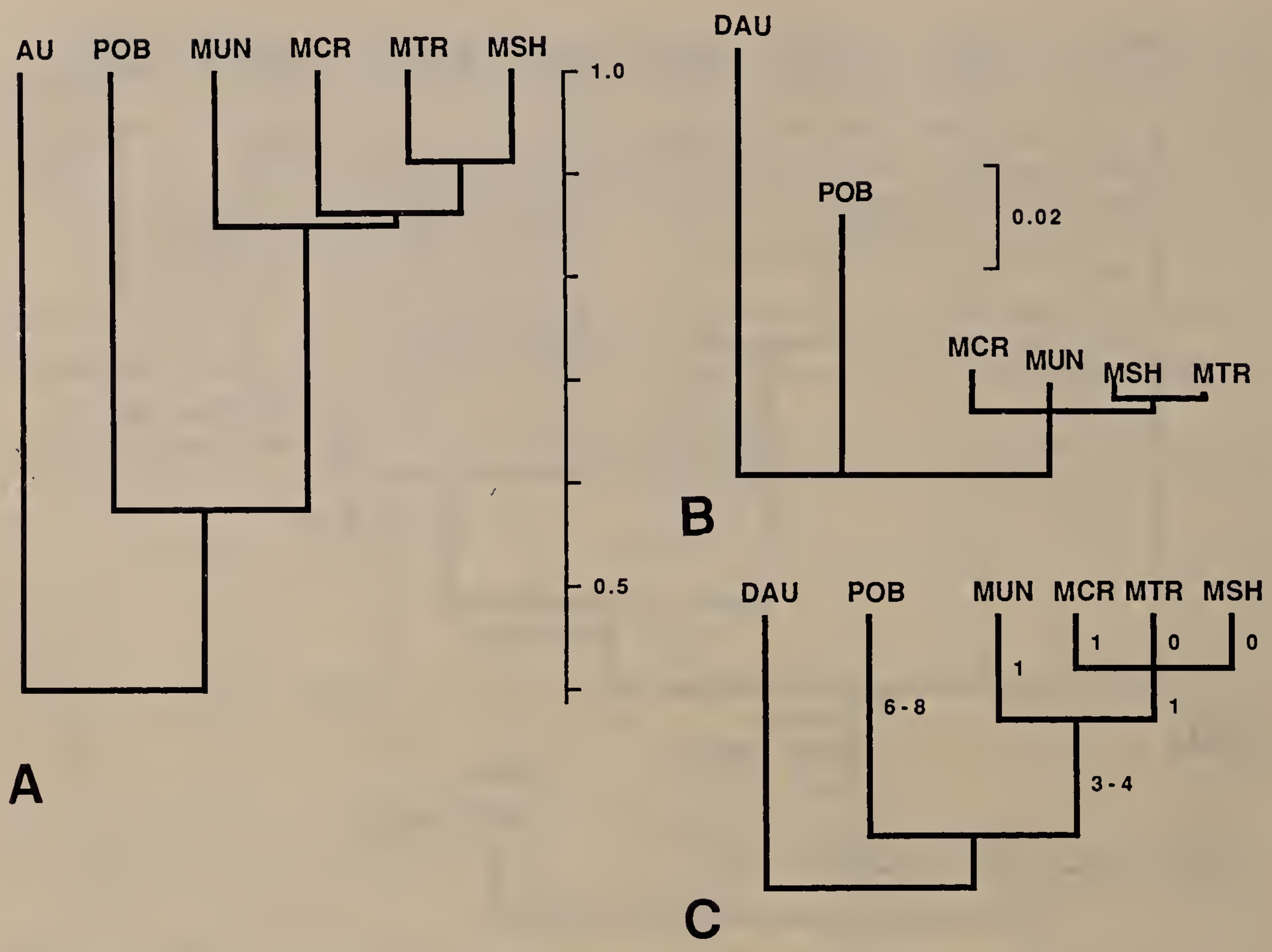

FIG. 4.—Three trees derived from the electrophoretic data: A) a UPGMA tree based on Rogers' similarity values (scale) generated from the allele frequency data; B) a tree based on the Fitch and Margoliash algorithm (1967) with the vertical axes representing branch lengths (indicative of divergence); C) a consensus tree based on cladistic analyses. Numbers indicate fixed differences. See text for discussion.

Desmodillus auricularis (Qumsiyeh and Chesser, 1988). Genetic distances (Rogers, 1972) for pair-wise comparisons of all taxa examined were used to construct a tree based on UPGMA (Fig. 4A). The lowest genetic distance value was between *M. shawi* and *M. tristrami* at 0.078, and all species of *Meriones* were closely clustered. The electrophoretic similarity among the four species of *Meriones* is corroborated by an analysis using the Fitch and Margoliash method (Fig. 4B). Cladistic analyses using a Wagner algorithm (Farris, 1970, 1978) (and optimized using MacClade) produced four tree topologies that could be distilled to a consensus tree (Fig. 4C). These latter cladistic analyses were performed using *Desmodillus* as an outgroup to *Meriones* and *Psammomys* for reasons discussed elsewhere (Qumsiyeh and Chesser, 1988).

All trees derived from the electrophoretic data show that the four species of *Meriones* shared a common ancestor after divergence of *Psammomys* (Fig. 4). Intrageneric relationships of *Meriones* are more difficult to resolve because of the high genetic similarity and the small number of specimens examined of the four species of the genus. However, none of these analyses allied *M. crassus* with *M. tristrami* as did the chromosomal analysis. The consensus tree in Figure 4C shows that *M. unguiculatus* was the first to branch from the *Meriones* lineage, with the other three species sharing a common ancestor.

Discussion

The use of electrophoretic data in systematics has been discussed at length by Avise (1974) and Buth (1984). The utility of these data in generating a rigorous phylogeny is limited by lack of knowledge about directions of change in electrophoretic mobilities and the small sample sizes used in my studies. The problem of small sample sizes in estimating genetic distances is somewhat ameliorated by increased numbers (32 in this study) of loci (Nei and Roychoudhuri, 1974). However, the problem of determining polarity in polymorphic loci is more serious (Qumsiyeh *et al.*, 1988). With these limitations in mind, the following conclusions about the electrophoretic data can be made. There was little differentiation among the four species of *Meriones*, but significant genic differences among *Desmodillus*, *Meriones*, and *Psammomys*. Within *Meriones*, a close association of *M. shawi*, *M. crassus*, and *M. tristrami* was manifested in both phenetic and cladistic analyses of the electrophoretic data (albeit no fixed differences). The electrophoretic data thus is concordant with previous hypotheses based on morphologic evidence in two aspects. First, previous authors (Chaworth-Musters and Ellerman, 1947; Corbet, 1978; Pavlinov, 1982) have agreed that the genus *Meriones* is a well-defined and monophyletic genus. Second, the divergence of *M. unguiculatus* from *M. shawi*, *M. crassus*, and *M. tristrami* also was suggested by the same studies.

Analyses of the G-band data using the outgroup method identified only a single synapomorphy for the genus *Meriones* (Fig. 3). This is in disagreement with analyses using the commonality criterion, which shows the genus *Meriones* as paraphyletic (Benazzou *et al.*, 1982*b*, 1984). All *Meriones* examined except *M. persicus* belong to the morphologically defined subgenus *Pallasiomys* (Chaworth-Musters and Ellerman, 1947). Clearly, *M. persicus* cannot be identified as distinct from the other five species on chromosomal grounds (Fig. 3). It would be interesting to obtain electrophoretic data for *M. persicus* to see if it can be distinguished by that method. The four species for which I had tissues are genetically similar (Fig. 4). In either case, if strict parsimony is followed, the chromosomal phylogeny would suggest that the morphologic change that defined the genus *Meriones* (Chaworth-Musters and Ellerman, 1947; Pavlinov, 1982) was accompanied by electrophoretic changes and few chromosomal changes. More importantly, a conflict exists between the chromosomal phylogeny (Fig. 3) and electrophoretic and morphologic data relating to the interrelationships of the four species of *Meriones* for which both electrophoretic and chromosomal data are available (*M. unguiculatus*, *M. shawi*, *M. crassus*, and *M. tristrami*). Chromosomally, two groups exist representing a low as opposed to a high diploid number (Fig. 3). Neither grouping is substantiated by either morphologic (Chaworth-Musters and Ellerman, 1947; Pavlinov, 1982) or (with the reservations discussed above) electrophoretic data (Fig. 4).

The chromsomal data presented demonstrate numerous homoplasies in Robertsonian rearrangements. As suggested earlier for another group of gerbils (Qumsiyeh *et al.*, 1987), this situation can be conducive to arriving at trees that are parsimonious, but not phylogenetically compatible, with other data sets. To alter the chromosomal tree, it is possible to postulate chromosomal synapomorphies (fusions) for *Meriones* that were lost subsequently (reversal) in some taxa. For example, the centric fusion events characterizing *M. unguiculatus*, *M. persicus*, *M. libycus*, and *M. shawi* (11/4d, 7/12, 5/33) also may have been present in the ancestor of *M. crassus* and *M. tristrami,* and susequently lost as a result of reversal events (fissions). Although this would be a less parsimonious explanation of the chromosomal data than the tree presented (Fig. 3), it is supported by several facts. First, both *M. crassus*, and *M. tristrami* underwent other independent fission events (for example in 3/4p and 13/14) and all or most of the chromosomes in these two species are acrocentric, resulting in high diploid numbers. Second, the tree in Figure 3 already shows numerous homoplasies in Robertsonian rearrangements. Thus, the arrangement of the taxa of *Meriones* can be altered with minimal additional homoplasies. Third, electrophoretic and morphological data sets generally support chromosomal phylogenies in mammals (Arnold *et al.*, 1982; Baker *et al.*, 1987; Qumsiyeh, 1988).

I postulate that the problems of determining relationships using Robertsonian rearrangements demonstrated here for *Meriones* and earlier for *Tatera* and *Gerbillurus* (Qumsiyeh *et al.*, 1987) can be explained by the nature of the rearrangements and in the limitations of the chromosomal G-band analysis. Each species has a limited number of chromosomal arms that could associate (fusions) or dissociate (fissions). This number of arms cannot change unless the species acquires other rearrangements than centric fusions and fissions (for example, pericentric inversions). A taxon with numerous acrocentric elements can produce descendants with differing metacentric chromosomes by centric fusions, a situation that results in monobrachial homology (Baker and Bickham, 1986; Capanna, 1982;

Moritz, 1986; Porter and Sites, 1986). These latter studies addressed the importance of monobrachial homology in establishing reproductive isolation (and potentially speciation) but did not address the possibility of centric fissions occurring subsequent to this differentiation. Robertsonian rearrangements are the most common types of chromosomal rearrangements observed in animals (White, 1978). Additionally, taxa developing monobrachial homology by fusions usually have few other chromosomal changes and little, if any, genic and morphologic change (see Baker and Bickham, 1986, for a review). The reverse process of fissions also would be expected to occur with little additional effect on the taxa involved.

Centric fissions are *a priori* less amenable to documentation by standard comparative cytogenetic methods than are centric fusions. This can be illustrated with a simplified hypothetical situation of Robertsonian fusions in a lineage with four unique autosomes (1-4). The ancestor could produce several descendents with unique chromosomal conditions (for example (1/2, 3/4), (1/3, 2/4), (1/3, 2, 4), and so on). However, if further evolution occurs by fissions in taxa with monobrachial homology, the resulting descendent taxa would have the same chromosomal condition (1, 2, 3, 4) even though the events were different fissions (for example, fission in 1/2 as compared to 1/3 above). Because a fission or a fusion event occuring in a natural population cannot be observed, we are limited to observing the chromosomal conditions in extant taxa that either have fissions (with little or no phylogenetic information) or fusions. Thus, fusions are retained as the informative data points for a chromosomal phylogeny because they can be traced to ancestral conditions. It is not surprising, therefore, that the simplest chromosomal explanations always involve grouping fissioned taxa (those with high diploid numbers) in more primitive branches.

Investigators, of course, are limited by the availability of additional data sets and, in the absence of such data sets, intermediate ancestors with monobrachial homology for taxa with high diploid numbers cannot be proposed. Combination of electrophoretic, morphologic, and chromosomal data thus has allowed illustration of two examples where homoplasy is underestimated when studying genera in which both high and low diploid numbers occur: 1) the relationships of *Gerbillurus* and *Tatera* (Qumsiyeh *et al.*, 1987), and 2) the relationships of species of *Meriones* discussed above.

Recently, a study of chromosome evolution in the family Canidae (Wayne *et al.*, 1987*a*, 1987*b*) also produced a dichotomy between high and low diploid number species. Wayne and O'Brien (1987) performed an electrophoretic analysis on the same group of mammals.

Although these authors did not discuss the conflict in the two data sets, this study provides another excellent example of a case of chromosomal fissions obscuring the phylogeny. This can be seen best by the phylogenetic position of the fennec (*Fennecus zerda*), which has a 2n = 64. In the chromosomal phylogeny, this species is associated with the "high numbered acrocentric species" as opposed to the "low numbered metacentric species," which include other foxes (Wayne *et al.*, 1987*b*). The chromosomal placement of the fennec could have been obscured in a similar fashion to that of gerbils with high diploid numbers because: 1) the fennec is morphologically nearer to other foxes (Van Gelder, 1978); 2) in an electrophoretic analysis, the fennec clearly can be associated with other foxes and is quite distant from canids with high diploid numbers (Wayne and O'Brien, 1987); and 3) the numerous fissions acquired in canid species (Todd, 1970; Wayne *et al.*, 1987*a*, 1987*b*). In light of the above discussion, similar re-analyses of published chromosomal phylogenies in combination with independent data sets on other groups of mammals with high and low diploid numbers would be prudent.

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APPENDIX.—*Allele frequencies for* Meriones *and* Psammomys. *Bold face indicates plesiomorphic conditions determined by comparison with data for* Desmodillus *(Qumsiyeh and Chesser, 1988). All other conditions are derived for* Meriones *and* Psammomys *or both, except for loci indicated by an asterix for which derived conditions could not be determined. Sample sizes in parentheses.*

Allele		*Meriones tristrami* (12)	*Meriones crassus* (3)	*Meriones unguiculatus* (2)	*Meriones shawi* (7)	*Psammomys* (9)
CON	**100**	1	1	1	1	.395
	95					.605
AK-1	100	.917	.833	1	.955	.947
	70	.083	.167		.045	.053
AK-2	**-100**	1	1	1	1	
	-150					1
ALB	-100	1	1	1	.455	
	-110				.545	1
CAT1B	200					1
	110	.056	.667	1	.818	
	100	.944	.333		.182	
CAT2W	100	.889	1	1	1	
	95	.111				
	60					1
CK-1	**100**	1	1	1	1	1
CK-2	**100**	1	1	1	1	1
CK-3	**100**	1	1	1	1	
DIA	110	.056	1	1	.955	
	100	.916				1
	95	.028			.045	
EST	**120**			1		1
	100	.778	.667		.273	
	105		.333			
	95	.222			.727	
*FUM	100	1	1	1	.364	
	-50				.636	1
*GOT-1	105			1		
	100	1	1		1	
	70					1
GOT-2	**-100**	1	1	1	1	
	-105					1
GLUD	**100**	.945	.333		.727	1
	95	.055	.667	1	.273	
α-GPD	**100**	1	1	1	1	1

APPENDIX. —*Continued.*

Allele		*Meriones tristrami* (12)	*Meriones crassus* (3)	*Meriones unguiculatus* (2)	*Meriones shawi* (7)	*Psammomys* (9)
ICD-1	**100**	1		1	1	1
	80		1			
ICD-2	**100**	1	1	1	1	1
LDH-1	**100**	1	1	1	1	1
LDH-2	**100**	1	1	1	1	1
MDH-1	**100**	1	1	1	1	1
MDH-2	**100**	1	1	1	1	1
MPI-1	**100**	1	1	1	1	1
MPI-2	**-100**	1	1	1	1	
	-90					1
PEP-A	**100**	1	1	1	1	
	95					1
PEP-B	**100**	1	1	1	1	
	90					1
*PEP-C	100	1	1	1	1	
	80					1
*6PGD-1	100	1	1	1	1	1
6PGD-2	**100**	1	1	1	1	.921
	90					.079
*PGM	200					1
	100	1	1	1	1	
SOD	140					1
	100	.945	1	1	1	
	50	.055				
TRF	**100**	.111	1	1	1	1
	98	.889				

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THE SYSTEMATIC STATUS OF TADARIDA BRASILIENSIS CYNOCEPHALA AND ANTILLEAN MEMBERS OF THE TADARIDA BRASILIENSIS GROUP, WITH COMMENTS ON THE GENERIC NAME RHIZOMOPS LEGENDRE.

Robert D. Owen, Ronald K. Chesser,
and Dilford C. Carter

The close relationship of members of the *brasiliensis* group of the free-tailed bat genus *Tadarida* long has been recognized. H. Allen (1864) made neither specific nor subspecific distinctions between the named taxa of the group. Later, when he (1893) revised his monograph of North American bats, Allen included *Nyctinomus mexicanus*, *N. murinus*, and *Nycticea cynocephala* in the synonomy of *Nyctinomus brasiliensis*. Also included in *N. brasiliensis* were bats from St. Kitts Island, British West Indies, later referred to *N. antillularum* Miller. Allen noted that specimens of *N. brasiliensis* from California possibly deserved variety status.

Bangs (1898), in applying the name *Nyctinomus cynocephalus* to Austroriparian free-tails, contended that the chances of *N. brasiliensis* and *N. cynocephalus* being the same were too remote to consider. However, Miller and Rehn (1901) regarded populations in California and the southeastern United States as subspecies (*N. b. californicus* and *N. b. cynocephalus*) of *N. brasiliensis*. *Nyctinomus mohavensis* Merriam (= *T. mexicana*), which they must not have seen, was given specific rank. G. M. Allen (1908) did not regard mainland populations of the group as warranting specific recognition, but he considered *N. antillularum* a distinct species. Later, however, Allen (1911) included in *N. brasiliensis* the subspecies *N. b. antillularum*, as well as *N. b. musculus* and *N. b. bahamensis*.

Lyon (1914) discussed the use of the name *Tadarida* in place of *Nyctinomus*, and subsequent authors have followed his opinion. Miller (1924) regarded the six named taxa of the group as separate species of *Tadarida*. Shamel (1931) recognized in the *brasiliensis* group the six species listed by Miller, included *T. murina* (omitted by Miller), and named two additional species, *T. intermedia* and *T. constanzae*. This arrangement was followed until Schwartz (1955) synonomized the nine species of Shamel on the basis that no structural differences distinguished one from any of the others, but he recognized each of the nine as subspecies of *T. brasiliensis*. Freeman (1981), in her morphometric comparison of 78 molossid species, followed Schwartz (1955) in taxonomic assignments within *T. brasiliensis*, considering *brasiliensis* to include the mainland races *mexicana* and *cynocephala*, as well as the Antillean populations.

A substantial body of evidence (Carter, 1962) led us to suspect that the taxonomic status of *T. b. cynocephala* deserved further evaluation. This study was undertaken, therefore, to examine the relationship of *T. b. cynocephala* to the species *T. brasiliensis*, with particular reference to two geographically adjacent subspecies, *T. b. mexicana* and *T. b. muscula*.

Comment on *Rhizomops* Legendre

In his thorough odontological analysis of *Tadarida* and related genera, Legendre (1984) proposed the generic name *Rhizomops*, comprised only of *R. brasiliensis* and presumably including all currently recognized subspecies. Although his methods were in a general way phylogenetically oriented, his recognition of *Rhizomops* was based entirely on plesiomorphic characteristics (see his figure 15 for summary of pertinent character states). Therefore, we view his recognition of generic status for the *brasiliensis* group to be unsupported. It is possible, of course, that synapomophies will be found eventually to resolve the basal fork in Legendre's figure 15, and we would point out that *Rhizomops* remains as an available name for the bats of the *brasiliensis* group should their generic status be supported appropriately. At the present time, however, we retain the use of *Tadarida* as the generic name for the *brasiliensis* group.

METHODS

Protein Electrophoretic Analysis

Tissue homogenate of heart and kidney was prepared from individual bats following the methods of Svoboda *et al.* (1985). Specimens examined for electrophoretic variation were from the following groups: *T. b. mexicana*—Waco, Texas (14), western Texas (3), western Oklahoma (2); *T. b. cynocephala*—Florida (14), North Carolina (14), Louisiana (12); *T. b. muscula*—Cuba (20); *T. b. murina*—Jamaica (14); *T. b. antillularum*—Dominica (18). Preliminary analysis of protein electrophoretic patterns indicated a fixed allelic difference between eastern and western mainland populations based on the esterase-2 locus. Therefore, all available specimens of *T. b. cynocephala* and from Antillean populations were compared to representative specimens of *T. b. mexicana* based upon this locus. Alleles were coded numerically with the ‘‘100’’ allele denoting the common allele for western (*T. b. mexicana*) populations, and all other alleles designated as to their mobility relative to the ‘‘100’’ allele.

Morphometric Analyses

A total of 1000 specimens of *T. b. cynocephala* (375), *T. b. mexicana* (584), and *T. b. brasiliensis* (41) was examined, and a maximum of 20 different skin and skull measurements for each specimen was taken (Carter, 1962). Those measurements used in this paper are skull length (greatest length of skull from occiput to and including the incisors); zygomatic breadth (greatest transverse dimension from outside borders of zygomatic arches); forearm (greatest distance from back of elbow to anteriormost border of wrist with wing folded); and fifth metacarpal (greatest linear dimension of that bone).

Bats were aged according to four classes: 0, adult bats with no macroscopically obvious toothwear; I, with obvious toothwear but less that one-third of the upper canines worn away; II, one-third or more but less than two-thirds of the canines worn away; III, two-thirds or more of the canines worn away. Care was taken to avoid misclassifying a bat with broken canines by checking the cheekteeth for obvious toothwear. The age classes are purely arbitrary and the time periods represented are not known. It is assumed, although without evidence other than that some bats seem relatively long-lived for small mammals (Cockrum, 1956; Hall *et al.*, 1957; Keen and Hitchcock, 1980), that each age class represents at least a three- to five-year period.

The effects of locality, sex, age class, and taxon on the observed variation of the variates were estimated with analysis of variance (ANOVA). The 0.01 level of probability (that the observations are due to randomness) was selected as the standard level of significance.

RESULTS

Protein Electrophoretic Analysis

Three alleles (100, 85, and 80) of the esterase-2 locus were observed over all *Tadarida* specimens examined. Genotypes for each specimen and allele frequencies for each population are presented in Table 1. All specimens of *T. b. mexicana* except one possessed the 100 allelle in some combination. All *T. b. cynocephala* possessed the 80 allelle, with two individuals from North Carolina and one from Louisiana being heterozygous with the 100 allele (100/80). All individuals from Cuba and Dominica were homozygous for the 80 allele. Another allele (85) was observed in the Jamaica and the Waco, Texas, populations. In Waco, a single specimen was homozygous for this allele (85/85) and three were heterozygotes (100/85). In contrast, half the Jamaican specimens were homozygous for the allele, with the remainder split about evenly between homozygous for 80 and heterozygotes of the two alleles.

Morphometric Analyses

Tadarida brasiliensis cynocephala can be distinguished from *T. b. mexicana* (and *T. b. brasiliensis*) based on skull length or zygomatic breadth (Tables 2 and 3). Carter (1962) discussed other aspects of morphology that serve to separate these two similar taxa, but all appear to be related to a general size factor. For additional information concerning morphometric relationships of *T. b. cynocephala* and *T. b. mexicana* populations, see Tables 4-12.

TABLE 1.—*Specimens examined, and electrophoretic mobility of the esterase-2 locus. Specimen numbers listed refer to the Texas Tech University frozen tissue (TK) catalog, except LJB numbers (donated by the Museum of Zoology, Louisiana State University). Waco specimens marked with an asterisk were taken on 3 April; all other Waco specimens were collected in winter (30 December-26 February). Specimens with only one allele listed were homozygous for that allele. Frequencies are presented as percentages for the 100, 85, and 80 alleles, respectively, for each population sample. Question mark indicates uncertainty in scoring that individual.*

Tadarida brasiliensis mexicana

Waco, Texas		Western Texas		Western Oklahoma	
21826	100	26303	100	24870	100
21827	100	26304	100	24902	100
21828	100	26540	100		
21829	100/85			(100/0/0)	
21830	85(?)	(100/0/0)			
21831	100				
*26599	100/85				
*26600	100/85				
26601	100				
26602	100				
26603	100				
26604	100				
26605	100				
26606	100				
(86/14/0)					

Tadarida brasiliensis cynocephala

Florida		North Carolina		Louisiana	
26635	80	21811	80	24825	80
26636	80	21812	80	24826	80
26637	80	21814	80	24827	80
26638	80	21815	100/80	24828	80
26639	80	21816	80	24829	80
26640	80	21817	80	24830	80
26641	80	21818	80	24831	80
26642	80	21819	100/80	24832	80
26643	80	21820	80	LJB 2100	80
26645	80	21821	80	LJB 2103	100/80
26646	80	21822	80	LJB 2105	80
26647	80	21823	80	LJB 2113	80
26648	80	21824	80		
26649	80	21825	80	(4/0/96)	
(0/0/100)		(7/0/93)			

TABLE 1.—*Continued.*

Tadarida brasiliensis muscula, Cuba		
32012 80	32065 80	32083 80
32059 80	32066 80	32092 80
32060 80	32067 80	32093 80
32061 80	32068 80	32094 80
32062 80	32069 80	32095 80
32063 80	32070 80	32096 80
32064 80	32071 80	
		(0/0/100)
Tadarida brasiliensis murina, Jamaica		
9232 85	9241 85	9247 80
9234 80	9242 80	9248 85/80
9235 85	9244 85/80	9250 85
9236 85	9245 85	26745 80
9239 85	9246 85/80	
		(0/61/39)
Tadarida brasiliensis antillularum, Dominica		
15504 80	15557 80	15563 80
15552 80	15558 80	15564 80
15553 80	15559 80	15565 80
15554 80	15560 80	15566 80
15555 80	15561 80	15567 80
15556 80	15562 80	15568 80
		(0/0/100)

DISCUSSION

Carter (1962) detailed a number of reasons for considering *cynocephala* to be a species separate from *brasiliensis* and from *mexicana*, which he also regarded as specifically distinct from *brasiliensis*. The morphometric data, some of which are compared in Tables 2 and 3, indicate that significant size differences exist between *T. b. cynocephala* and *T. b. mexicana*, with *cynocephala* being larger in the two crainal variates considered. In addition to morphometric data, Carter's (1962) evidence included physiological, distributional, ecological, and behavioral attributes of the two taxa. These will not be reiterated here, other than to point out that they comprised a rather compelling body of evidence for specific recognition of *cynocephala*.

Electrophoretic evidence presented herein indicates that there is an apparent allelic difference that effectively separates *T. b. mexicana* from *T. b. cynocephala* and the Antillean populations. The three occurrences of the *mexicana* (100) esterase-2 allele in

TABLE 2.—*Comparison of measurement data for skull length of* T. b. cynocephala, T. b. mexicana, *and* T. b. brasiliensis.

Subspecies	Sex	N	Min.	Max.	$\bar{X}$	s	CV
T. b. cynocephala	♂	128	16.7	18.4	17.48	.307	1.75
T. b. mexicana	♂	173	16.2	17.7	16.94	.308	1.81
T. b. brasiliensis	♀♂	41	16.1	17.8	17.28	.400	2.31
Main effect	d.f.		MS		F		P
Subspecies	2		10.68		104		<.001
T. b. cynocephala	♀	152	16.1	18.2	17.16	.306	1.78
T. b. mexicana	♀	164	16.1	17.4	16.72	.274	1.63
T. b. brasiliensis	♀♂	41	16.1	17.8	17.28	.400	2.31
Main Effect	d.f.		MS		F		P
Subspecies	2		9.99		107		<.001

TABLE 3.—*Comparison of measurement data for zygomatic breadth of* T. b. cynocephala, T. b. mexicana, *and* T. b. brasiliensis.

Subspecies	Sex	N	Min.	Max.	$\bar{X}$	s	CV
T. b. cynocephala	♂	123	9.6	10.8	10.27	.211	2.05
T. b. mexicana	♂	162	9.3	10.4	9.78	.186	1.90
T. b. brasiliensis	♀♂	32	9.1	10.5	9.95	.282	2.83
Main effect	d.f.		MS		F		P
Subspecies	2		8.36		192		<.001
T. b. cynocephala	♀	144	9.6	10.6	10.10	.189	1.87
T. b. mexicana	♀	104	9.3	10.2	9.70	.159	1.64
T. b. brasiliensis	♀♂	32	9.1	10.5	9.95	.282	2.83
Main effect	d.f.		MS		F		P
Subspecies	2		4.64		125		<.001

specimens of *cynocephala* sampled may or may not represent genetic introgression from populations of *mexicana*. It is important also to note that the *cynocephala* (80) allele was not found either in our *mexicana* samples (Table 1), or in those of Svoboda *et al.* (1985), which included 164 specimens of *T. b. mexicana* (our 80 allele is slower than any of the three esterase-2 alleles reported in their paper).

Several lines of evidence appear to point to the specific status of *cynocephala*, perhaps with the inclusion of the Antillean populations: 1) the evidence detailed by Carter (1962), including the

TABLE 4.—*Measurement data for skull length of* T. b. cynocephala.

Locality	N	Min.	Max.	$\bar{X}$	$CI_{\bar{x}}$	s	CV
			Males				
Small samples, Georgia-Florida	15	17.0	17.8	17.32	.177	.231	1.33
Glennville, Georgia	14	17.0	18.1	17.46	.252	.313	1.79
Butler, Alabama	11	17.2	17.8	17.49	.216	.226	1.29
Brookhaven, Mississippi	14	17.1	18.0	17.61	.235	.292	1.65
Palestine, Texas	11	16.7	17.7	17.24	.301	.315	1.82
Pineland, Texas	77	16.7	18.4	17.51	.093	.309	1.76
Main effect	d.f		MS		F		P
Localities	5		0.272		3.12		.02
			Females				
Small samples, Georgia-Florida	22	16.7	17.8	17.22	.196	.325	1.88
Ocheesee, Florida	24	16.8	17.6	17.21	.142	.249	1.44
Colquitt, Georgia	30	16.5	17.7	17.12	.153	.303	1.76
Butler, Alabama	18	16.9	17.6	17.20	.120	.176	1.02
Pineland, Texas	58	16.1	18.2	17.14	.123	.352	2.05
Main effect	d.f.		MS		F		P
Localities	4		0.057		0.60		>.20
Sexes	1		6.900		73.17		<.01

TABLE 5.—*Measurement data for skull length of* T. b. cynocephala *collected at Pineland, Texas, 13 April 1961.*

Age class	N	Min.	Max.	$\bar{X}$	$CI_{\bar{x}}$	s	CV
			Males				
0	37	16.7	18.1	17.38	.138	.310	1.78
I	26	17.1	18.4	17.63	.146	.268	1.52
Main effect	d.f.		MS		F		P
Age class	1		0.940		10.90		<.01
			Females				
0	23	16.9	18.2	17.19	.167	.285	1.65
I	20	16.1	17.6	17.00	.219	.345	2.01
Main effect	d.f.		MS		F		P
Age class	1		0.390		3.88		.11

morphometric data presented herein, concerning the differences between *cynocephala* and the other mainland taxa (particularly

TABLE 6.—*Measurement data for zygomatic breadth of* T. b. cynocephala.

Locality	N	Min.	Max.	$\bar{X}$	$CI_{\bar{x}}$	s	CV
			Males				
Small samples, Georgia-Florida	12	9.6	10.5	10.11	.183	.204	2.01
Glennville, Georgia	14	10.0	10.5	10.25	.122	.152	1.48
Butler, Alabama	11	10.0	10.6	10.27	.181	.190	1.85
Palestine, Texas	9	9.9	10.4	10.13	.237	.224	2.21
Pineland, Texas	77	9.7	10.8	10.31	.065	.213	2.06
Main effect	d.f.		MS		F		P
Localities	4		0.152		3.69		.01
			Females				
Small samples, Georgia-Florida	17	9.7	10.6	10.13	.165	.234	2.30
Ocheesee, Florida	24	9.9	10.4	10.09	.076	.135	1.31
Colquitt, Georgia	30	9.8	10.5	10.15	.079	.157	1.54
Butler, Alabama	15	9.9	10.4	10.13	.142	.185	1.82
Pineland, Texas	58	9.6	10.5	10.04	.071	.204	2.03
Main effect	d.f.		MS		F		P
Localities	4		0.072		2.08		.15
Sexes	1		2.060		51.50		<.01

TABLE 7.—*Measurement data for forearm of* T. b. cynocephala.

Locality	Sex	N	Min.	Max.	$\bar{X}$	$CI_{\bar{x}}$	s	CV
Merrits Island, Florida	♀♂	32	40.4	43.8	41.62	.401	.827	1.98
Panacea, Florida	♀♂	28	40.2	43.2	41.86	.526	1.005	2.40
Ocheesee, Florida	♀♂	48	40.2	43.8	42.22	.319	.826	1.95
Glennville, Georgia	♀♂	19	40.2	43.7	42.01	.627	.952	2.26
Colquitt, Georgia	♀♂	32	40.4	44.3	41.97	.469	.969	2.30
Butler, Alabama	♀♂	29	41.1	44.1	42.34	.453	.885	2.09
Brookhaven, Mississippi	♀♂	22	40.6	43.4	41.84	.484	.802	1.91
Palestine, Texas	♂	12	41.0	44.2	42.92	.919	1.025	2.38
Pineland, Texas	♂	76	40.0	44.8	42.30	.293	.956	2.26
Pineland, Texas	♀	64	39.5	43.9	42.17	.327	.982	2.32
Main effect	d.f.			MS		F		P
Localities	9			2.800		3.25		<.01
Sexes (Pineland)	1			0.610		0.650		>.20

mexicana); 2) the wide geographic separation of the southernmost Antillean populations (St. Lucia—Jones and Phillips, 1970;

TABLE 8.—*Measurement data for fifth metacarpal of* T. b. cynocephala. *Males and females present in all samples.*

Locality	N	Min.	Max.	$\bar{X}$	$\mathrm{CI}_{\bar{x}}$	s	CV
Merrits Island, Florida	45	23.0	25.4	24.38	.250	.624	2.55
Panacea, Florida	28	23.8	26.0	24.86	.296	.566	2.27
Ocheesee, Florida	48	23.1	27.2	25.05	.314	.814	3.24
Glennville, Georgia	19	23.6	26.4	24.94	.515	.781	3.13
Colquitt, Georgia	32	22.4	26.8	24.52	.500	1.034	4.21
Butler, Alabama	29	23.2	26.6	24.79	.470	.916	3.69
Brookhaven, Missippi	22	23.0	26.4	24.57	.481	.800	3.25
Palestine, Texas	12	23.6	27.5	25.11	.913	1.019	4.05
Pineland, Texas	140	22.4	26.5	24.82	.163	.748	3.01

Main effect	d.f.	MS	F	P
Localities	8	2.000	3.22	<.01
Sexes (Pineland)	1	0.560	1.00	>.20

TABLE 9.—*Geographic distribution of the sample means for the forearm and fifth metacarpal of* T. b. cynocephala. *Grand mean for forearm is 42.12; for fifth metacarpal, 24.77.*

Forearm		Fifth Metacarpal	
$\bar{X}$	Locality (Year)	$\bar{X}$	Locality (Year)
41.62	Merrits Island, Florida (1923)	24.38	Merrits Island, Florida (1923)
41.84	Brookhaven, Mississippi (1937)	24.32	Colquitt, Georgia (1959)
41.86	Panacea, Florida (1958)	24.57	Brookhaven, Mississippi (1937)
41.97	Colquitt, Georgia (1959)	24.79	Butler, Alabama (1959)
42.01	Glennville, Georgia (1959)	24.82	Pineland, Texas (♂♂ + ♀♀) (1958-61)
42.17	Pineland, Texas (♀♀) (1958-61)		
42.22	Ocheesee, Florida (1959)	24.86	Panacea, Florida (1958)
42.30	Pineland, Texas (♂♂) (1958-61)	24.94	Glennville, Georgia (1959)
42.34	Butler, Alabama (1959)	25.05	Ocheesee, Florida (1959)
42.92	Palestine, Texas (1959)	25.11	Palestine, Texas (1959)

Varona, 1974; Baker and Genoways, 1978; Jones, 1990) from those nearest on the South American mainland (western Venezuela—Koopman, 1982); and 3) the populational differences in the esterase-2 protein locus, presented herein. Based on this evidence, we think it likely that *T. b. cynocephala* and the Antillean populations are isolated reproductively from

TABLE 10.—*Measurement data for skull length of* T. b. mexicana.

Locality	N	Min.	Max.	$\bar{X}$	$CI_{\bar{x}}$	s	CV
			Males				
Nogales, Arizona	14	16.5	17.4	16.96	.247	.307	1.81
Arizona	31	16.5	17.4	16.94	.132	.268	1.58
Grimes Co., Texas	9	16.4	17.7	17.23	.419	.375	2.18
Durango, México	21	16.4	17.6	17.06	.196	.317	1.86
Sinaloa, México	26	16.2	17.5	16.86	.160	.294	1.74
Michoacán, México	19	16.5	17.4	16.97	.177	.268	1.58
Chiapas, México	42	16.3	17.5	16.89	.135	.327	1.94
Chimaltinago, Guatemala	11	16.5	17.2	16.81	.202	.212	1.26
Main effect	d.f.		MS		F		P
Localities	7		0.224		2.49		.035
			Females				
Cochise Co., Arizona	9	16.5	17.2	16.85	.265	.237	1.41
Pima Co., Arizona	23	16.2	17.0	16.62	.130	.222	1.34
Arizona	33	16.2	17.2	16.69	.122	.254	1.52
Grimes Co., Texas	9	16.3	17.4	16.87	.479	.430	2.55
Durango, México	26	16.2	17.4	16.75	.166	.304	1.81
Sinaloa, México	22	16.1	17.1	16.59	.157	.261	1.57
Michoacán, México	23	16.2	17.2	16.76	.161	.275	1.64
Chiapas, México	19	16.4	17.2	16.77	.133	.202	1.20
Main effect	d.f.		MS		F		P
Localities	7		0.160		2.23		.06
Sexes	1		4.260		49.71		$<.01$

other taxa of *T. brasiliensis*. Additionally, we note the work of previous authors (particularly Shamel, 1931) who pointed out that considerable external and morphometric differences serve to distinguish *T. b. cynocephala* from Antillean populations.

Notwithstanding these conclusions, we do not believe that sufficient evidence is yet available concerning the species limits of *cynocephala* with respect to either the adjacent mainland or insular populations. Resolution of this issue is critical not only to our understanding of the evolution and biogeography of the *T. brasiliensis* group, but also to the nomenclature. Assuming that *cynocephala* is specifically distinct from *mexicana*, then the name *brasiliensis* probably would not be applicable to the *cynocephala* bats. If these prove also to be specifically distinct from Antillean bats, then the name *cynocephala* Le Conte, 1831, is certainly applicable at the specific level. If, on the other hand, *cynocephala*

TABLE 11.—*Measurement data for zygomatic breadth of* T. b. mexicana.

Locality	N	Min.	Max.	$\bar{X}$	$\text{CI}_{\bar{x}}$	s	CV
			Males				
Sta. Cruz Co., Arizona	13	9.5	10.1	9.71	.152	.180	1.85
Arizona	31	9.4	10.1	9.75	.094	.190	1.95
Grimes Co., Texas	8	9.6	10.4	9.92	.317	.256	2.58
Durango, México	21	9.5	10.3	9.87	.131	.211	2.14
Sinaloa, México	24	9.3	10.0	9.75	.102	.179	1.84
Michoacán, Mexico	17	9.6	10.1	9.80	.093	.132	1.35
Chiapas, México	37	9.5	10.2	9.78	.072	.161	1.65
Guatemala	11	9.5	10.0	9.74	.183	.192	1.97
Main effect	d.f.		MS		F		P
Localities	7		0.067		2.00		.10
			Females				
Pima Co., Arizona	17	9.3	9.9	9.68	.108	.152	1.57
Grimes Co., Texas	7	9.4	10.1	9.75	.352	.251	2.57
Durango, México	25	9.3	10.2	9.69	.093	.167	1.72
Sinaloa, México	17	9.4	9.9	9.65	.088	.125	1.30
Michoacán, México	21	9.3	10.0	9.74	.094	.151	1.55
Chiapas, México	17	9.4	10.0	9.71	.109	.155	1.60
Main effect	d.f.		MS		F		P
Localities	5		0.020		0.775		>.20
Sexes	1		0.400		12.78		<.01

populations are conspecific with those of the Greater Antilles, the name *murina* Gray, 1827, would have priority.

An alternate possibility to consider is that bats referred to *cynocephala* are specifically distinct from adjacent *mexicana* populations but not from those west coast populations of *mexicana* that are nonmigratory. These, and all nonmigratory populations in western North America, Central America, and South America might be conspecific, in which case the specific name *brasiliensis* would apply to the *cynocephala* bats but not to migratory populations of *mexicana*. Because of these diverse and unresolved issues concerning the affinities of *cynocephala*, in the interest of nomenclatorial stability we follow current taxonomic opinion (Wilkins, 1989) until clearer evidence is available. The relevant synonomy and other taxonomic and biological information concerning *Tadarida brasiliensis cynocephala* are presented here.

TABLE 12.—*Measurement data for forearm of* T. b. mexicana.

Locality	Sex	N	Min.	Max.	$\bar{X}$	$CI_{\bar{x}}$	s	CV
Frio Cave, Texas	♀♂	42	40.7	45.8	42.81	.465	1.114	2.60
La Boca Cave, Nuevo León, México	♀♂	55	40.8	45.4	42.95	.342	.949	2.21
España Cave, Durango, México	♀♂	98	41.0	45.9	43.03	.259	.975	2.26
España Cave, Durango, México	♀♂	35	41.0	44.5	42.56	.426	.926	2.18
Chinacaterra Cave, Sinaloa, México	♀♂	82	40.4	44.6	42.71	.314	1.077	2.52
Calaya, Guanajuato, México	♂	15	40.8	44.8	42.87	.789	1.025	2.39
Janitzio, Michoacán, México	♀♂	48	40.6	45.6	43.07	.389	1.000	2.32
Jalisco, México	♀♂	30	40.2	44.2	42.41	.546	1.086	2.56
Zapaluta Cave, Chiapas, México	♂	51	40.7	45.5	42.94	.129	.346	0.80
Zapaluta Cave, Chiapas, México	♀	128	38.7	45.2	42.84	.187	.812	1.90

Main effect	d.f.	MS	F	P
Localities	9	1.852	2.118	.04

Tadarida brasiliensis cynocephala (Le Conte)

Nyct[icea] cynocephala Le Conte, in McMurtrie's Cuvier, 1831, Animal kingdom, 1:432 (type locality—probably near Riceboro, Liberty Co., Georgia; type not designated).

Molossus cynocephalus, Cooper, 1837, Ann. Lyceum Nat. Hist. New York, 4:65, pl. 3, figs. 1 and 2.

Molossus fuliginosus Cooper, 1837, Ann. Lyceum Nat. Hist. New York, 4:67, pl. 3, figs. 3 and 4 (type locality—Miledgeville, Georgia; type not known to be in existence). One specimen was sent to the Lyceum of Natural History; it differed from *M. cynocephalus* in having four rather than six lower incisors and in having smooth rather than crimped ears.

Rhinopoma carolinense, Le Conte (not Geoffroy St.-Hilaire), 1855, Proc. Acad. Nat. Sci. Philadelphia, 7:437-438. Le Conte's citation of Geoffroy (1829, Dict. de Sciences Naturales, p. 45) was an error, but Le Conte believed that this bat was from North America and had priority—his source of reference may have been Gundlach (1840, Arch. Naturgeschichte, p. 358). Tomes (1861, Proc. Zool. Soc. London, pp. 68-69) examined the type in the Paris Museum and discovered that an accidental exchange of labels had occurred between a small African molossid and a *Lasiurus borealis* from North America.

Nyctinomus nasutus, Tomes, 1861, Proc. Zool. Soc. London, pp. 68-69 (part). Tomes (not H. Allen, 1864, Smiths. Misc. Coll., 165:7) was the first to use this name combination; it was based on the belief that *N. cynocephala* Le Conte was a synonym of *Molossus nasutus* Spix.

Nyctinomus brasiliensis, H. Allen, 1893 (not True, 1884), Bull. U. S. Nat. Mus., 43:163-171 (part). True (1884, Proc. U. S. Nat. Mus., 7:603) stated that the distribution of *N. brasiliensis* is Kansas and California to Chile and thereby excluded *T. cynocephala*.

Nyctinomus cynocephalus, Bangs, 1898, Proc. Boston Soc. Nat. Hist., 28:218.

Tadarida cynocephala, Miller, 1924, Bull. U. S. Nat. Mus., 128:85.

Tadarida brasiliensis cynocephala, Schwartz, 1955, J. Mamm., 36:106-109.

Type Locality.—Probably the Le Conte plantation, near Riceboro, Liberty Co., Georgia. No type was designated but what appears to be an original specimen (USNM 4742) collected by J. E. Le Conte is deposited in the United States National Museum of Natural History (Poole and Schantz, 1942).

Geographic Distribution.—From Harnett County, North Carolina (Lee and Marsh, 1978), south along the Atlantic coast through Florida at least as far south as Miami, west through Georgia, Alabama, Mississippi, and Louisiana to eastern Texas (Spenrath and LaVal, 1974), and north and west as far as Conway and Hot Springs, Arkansas (Saugey *et al.*, 1988). Additional isolated records have been reported from Ohio (Smith and Goodpaster, 1960; Mills, 1971) and Kentucky (Barbour and Davis, 1974).

Diagnosis.—*T. b. cynocephala* is similar in size and perhaps in habits to *T. b. brasiliensis* (perhaps only in part), but it averages larger than *T. b. mexicana* and *T. b. muscula* in many variates (Shamel, 1931). Series of specimens can be determined on the basis of skull length and zygomatic breadth (Tables 2 and 3; see also Tables 4, 6, 10, and 11). It is a sedentary, colonial species that utilizes buildings and hollow trees as diurnal roosts, and may be inactive at times, or even hibernate, during the winter.

Variation.—Sexual dimorphism occurs with respect to the cranial variates analyzed. The skulls of males average larger than those of females and the differences between the means are significant (Tables 4 and 6). The forearm and fifth metacarpal evidently are not sexually dimorphic elements (Tables 7 and 8).

Individual variation is low for all variates tested. The length of the fifth metacarpal is the most variable, but it is still less variable than is normal for linear dimensions of anatomical elements of mammals (Simpson *et al.*, 1961:91).

A large sample of males taken at Pineland, Texas, in April 1961 contains two age classes of adults. The younger males (class 0) average smaller in skull length than the older individuals (class I), and the means are significantly different (Table 5). Such a difference between age classes of females from Pineland is not demonstrated. Because most samples (representing localities) were not large enough to allow a segregation of age classes, the effect of locality may be confounded with an effect of age class.

Locality has no significant effect on differences between sample means of skull length and zygomatic breadth (Tables 4 and 6), although for both characters males show a nearly significant effect. For length of the forearm and the fifth metacarpal, locality has a significant effect (Tables 7 and 8). Neither the array for mean lengths of the forearm nor that for means of the fifth metacarpal is correlated with the geographic position of localities. Further, the two arrays do not correspond closely to each other with regard to locality. The locality effect does not seem to constitute a geographic cline; rather, the observed geographic variation seems to be only of a random nature.

Biogeography and Evolutionary History.—*T. b. cynocephala* occasionally is found roosting in hollow trees (Carter, 1962), and it is likely that this species was strictly tree-dwelling before buildings became available. The shift from trees to man-made structures as roosting sites obviously was not a difficult transition, because the bats now are found most commonly in buildings. The northern distribution of the species probably is limited by unfavorable winter conditions. Inasmuch as *T. b. cynocephala* overwinters in unheated buildings or in hollow trees, neither of which would be well protected against severely cold weather over a prolonged period of time, the subspecies probably is restricted to the southeastern United States where winters are relatively mild and where subfreezing conditions seldom last for more than a few days. The occurrence of populations as far north as North Carolina and Arkansas and as far west as eastern Texas may represent a post-Pleistocene expansion of the late Pleistocene distribution.

The western limit of this bat's geographic distribution generally conforms with the western limit of the pine-hardwood forest region of the southeastern United States. It is in this region that a seasonal overlap may occur between *T. b. cynocephala* and *T. b. mexicana* (Carter, 1962; Spenrath and LaVal, 1974; Glass, 1982). Although we cannot completely exclude the possibility of gene flow between *cynocephala* and *mexicana*, we emphasize that at most it appears to be minimal and unidirectional. Of the 40 specimens of *cynocephala* that we examined electrophoretically, the 100 allele was found three times, each time as a heterozygote.

Of the 19 *mexicana* that we examined and the 164 specimens examined by Svoboda *et al.* (1985), none possesed the 80 allele. Carter (1962) and Spenrath and LaVal (1974) pointed out that the populations most critical to evaluating the possibility of gene flow between these two taxa are those found in, and southeast of, Brazos County, Texas. Certainly, intensive collecting and analysis of specimens from eastern Texas and western Louisiana will be needed to resolve this question.

Regardless of that outcome, the problem remains concerning the relationship of *cynocephala* to the various populations in the Greater and Lesser Antilles. Each of the three island populations we sampled (from Cuba, Jamaica, and Dominica) shared the 80 allele with *cynocephala*, and in fact those from Cuba and Dominica appear to be monomorphic for that allele. Whether these populations are conspecific with *cynocephala* must be ascertained based on other evidence, but the important point is that the 80 allele appears to be a synapomorphy uniting *cynocephala* and the Antillean bats. The question of the origin of these bats is probably quite germane to the more general questions of Antillean zoogeography. Generally it is assumed that three possible invasion routes have been available for volant animals to colonize the Antilles: 1) from North America, through Florida; 2) from Central America, through the Yucatán Peninsula; and 3) from South America, through Trinidad. Although *T. brasiliensis* does not currently occupy the Yucatán Peninsula or Venezuela except in the far west, it is possible that it did occur in those areas at times when colonization took place. Clearly, the presence of the 80 allele in populations from México south of the Isthmus of Tehuantepec, from Central America, or from northern South America, would provide insight into the zoogeographic history of these bats.

If in fact *cynocephala* is found to have originated from Antillean populations, the area of contact in eastern Texas would be a zone of secondary contact, and, therefore, would be especially important to evaluate. If genetic introgression is occuring there, and is in fact unidirectional, this provides an excellent natural situation in which to evaluate genetic mechanisms involved in speciation events (Baker *et al.*, 1989). If no gene flow is found to occur in the area of sympatry or parapatry, pre- and postmating isolating mechanisms may be evaluated in these populations.

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